

## Growth, Leaf Characteristics, and Spore Production in Native and Invasive Tree Ferns in Hawaii

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**ABSTRACT.**—The Australian tree fern *Sphaeropteris cooperi* is an invasive species in Hawaiian wet forests where it displaces *Cibotium*, the dominant native Hawaiian tree fern, where they co-occur. This study was undertaken in order to assess the relative growth rates and reproductive potential of *S. cooperi* and the native *Cibotium* species. Field measurements of growth rates, fertile frond production and leaf traits were made monthly over the course of one year. *Sphaeropteris cooperi* had a significantly higher growth rate, both in terms of height increase and frond production, and maintained four times more fronds than the native *Cibotium* species. The mean annual height increase of the invasive tree fern was 15 cm compared to 2 to 3 cm for the native tree ferns. The leaf mass per area of *S. cooperi* was significantly lower than that of the native *Cibotium* species, and the leaf life span was significantly shorter, suggesting that the cost of construction of the invasive species' fronds was relatively low. *Sphaeropteris cooperi* also produced significantly more fertile fronds per month than the native tree ferns. These differences in life history characteristics may help explain the rapid spread and success of *S. cooperi* in Hawaii.

The invasion of non-native plants into native ecosystems has become a topic of great concern in recent years, particularly in isolated island ecosystems such as the Hawaiian Islands (Loope and Mueller-Dombois 1989, Vitousek et al. 1987). Of the more than 800 introduced plant species which have become naturalized in the Hawaiian Islands, 30 are ferns (Vitousek et al. 1987, Wagner 1995). The Australian tree fern, *Sphaeropteris cooperi* (Hook. ex F. Muell.) Tryon [syn. *Cyathea cooperi* (Hook. ex F. Muel.) Dom.], was introduced to the Hawaiian Islands as a horticultural plant and first escaped from cultivation in the 1950s (Wagner 1995). *Sphaeropteris cooperi* is now naturalized on the islands of Oahu, Maui, Kauai, and Hawaii (Wagner 1995) and is listed as among the worst alien plant invaders of Haleakala National Park (Loope et al. 1992).

Tree ferns in the genus *Cibotium* are the dominant native tree ferns in Hawaii. There are four endemic species in this genus, three of which (*C. chamissoi* Kaulf., *C. menziesii* Hook., *C. glaucum* [Sm] Hook. and Arn.) are found on all of the major islands. The fourth (*C. nealii* Degener) is found only on the island of Kauai (Palmer 1994). These endemic ferns grow in semi-wet to wet forests from an elevation of 40 m to 1800 m, and at a mean annual temperature range between 13°C and 23°C (Becker 1976). In the Hawaiian forests, tree ferns are keystone species which have a substantial impact on the structure and function of the forest around them. For example, the native *Cibotium* support native Hawaiian plants as epiphytes (Medeiros et al. 1993), as well as serving as nurse logs for a number of native species which become established on the well-aerated adventitious roots of the tree ferns' trunk (Buck 1982). The native

TABLE 1. Elevation (m), annual precipitation (mm), tree fern species present, and the number of individuals studied (n) at the sites used for this study. Lyon Arboretum, Wa'ahila Ridge and Mt. Ka'ala are on the island of O'ahu, Waineke Swamp is on the island of Kauai.

Site	Elevation (m)	Rainfall (mm)	Species	Sample size (n)
Low elevation (Lyon Arboretum)	155	4000	<i>Sphaeropteris cooperi</i>	6
			<i>Cibotium chamissoi</i>	8
Mid elevation (Wa'ahila Ridge)	430	2000	<i>Cibotium chamissoi</i>	6
			<i>Cibotium menziesii</i>	6
High elevation (Mt. Ka'ala bog)	1225	2000	<i>Cibotium chamissoi</i>	8
			<i>Cibotium menziesii</i>	8
			<i>Cibotium glaucum</i>	8
High elevation (Waineke Swamp)	1250	2000	<i>Sphaeropteris cooperi</i>	6

tree ferns also sequester high levels of nitrogen and phosphorus in their leaves compared to other native Hawaiian rainforest species (Vitousek et al. 1995).

This study was undertaken in order to assess the relative growth rates and reproductive potential of the native *Cibotium* and the invasive *Sphaeropteris cooperi*. We hypothesize that the invasive *S. cooperi* has faster growth rates and a greater spore production than the native tree ferns. In addition, we hypothesize that the invasive tree ferns produce fronds and spores more consistently throughout the year than the native ferns. This difference in growth and reproductive capacity may contribute to the ability of *S. cooperi* to outcompete the native tree ferns in Hawaiian rainforests. We also predict that the invasive tree fern, consistent with what has been observed in other invasive species in Hawaii (Baruch and Goldstein 1999), will have a shorter leaf life span and lower leaf mass per area (LMA) than the native tree ferns. The native *Cibotium* species were chosen for comparison based on their similar growth form and phylogenetic relatedness to the Australian tree fern. By studying native and invasive species of similar growth form that grow in the same habitat, predictions as to the relative growth and reproductive performance of the invasive and native plants can be drawn.

MATERIALS AND METHODS

STUDY SITES.—Four sites were selected for this study based on accessibility and species composition (Table 1). The range of elevations of the sites, from 200 m to 1250 m, encompasses much of the elevational range of the native Hawaiian tree ferns. The tree ferns at each site were growing under similar substrate and environmental conditions. All sites were tree dominated with an understory of ferns and tree ferns. The tree ferns at the two high elevation sites were located in relatively well drained soils at the edge of a bog. Individual plants of the same size class (1.5 m to 2.0 m) were randomly selected, and comparisons were made between individuals of the invasive and native tree ferns from the shaded understory. Six to eight individuals of each species at each

site were studied (Table 1). The low elevation site was the only accessible site with sympatric native and invasive tree ferns, and the only site where the invasive tree fern was available for a long enough period of time to measure growth. The high elevation site on Oahu contained only native tree ferns. An additional site on Kauai with similar elevation and rainfall was selected for comparison. *Sphaeropteris cooperi* is naturalized at this site, but *Cibotium chamissoi*, *C. menziesii*, and *C. glaucum* were not found. Due to management efforts to control *Sphaeropteris cooperi*, this plant was not available at all sites. This fact, and the fact that sample sizes were relatively small, led us to be cautious when making extrapolations based on the results of this study.

**GROWTH MEASUREMENTS.**—Stem growth rate, frond production, and leaf life span were monitored for 12 consecutive months, from November 1997 through October 1998, on mature sporophytes of the same size class at the Lyon Arboretum, Waahila Ridge and Mt. Kaala sites. It was not possible to measure growth and leaf life span on the high elevation population of *S. cooperi* as management efforts to control this plant resulted in their removal before measurements could be completed. A point at the soil surface on one side of each tree fern was marked and measurements of stem height from the meristem to this point were taken monthly. All newly emerging fronds were flagged, dated and monitored until senescence. The number of months between frond emergence and senescence was recorded as the life span of the frond.

**LEAF TRAITS.**—The total number of living fronds was counted monthly. For the purposes of this study, a frond was defined as living when it had more than 10% green tissue remaining. The mean surface area per frond was estimated by multiplying the total number of pinnules per frond by the average surface area of a pinnule. Ten pinnules per frond were collected, and the surface area of each pinnule was measured with a Licor 3000A area meter (Licor, Inc., Lincoln, Nebraska) and averaged. The surface area of the tip of each frond was measured separately, as the pinnules in this region were smaller. The average surface area per frond was multiplied by the number of mature living fronds per plant to estimate the total leaf surface area per plant.

Tissue samples from the middle of a frond were collected in the field for leaf mass per area (LMA) estimates. Samples were kept in a cooler for less than 24 hours until they could be returned to the laboratory, at which time the area was measured using a LI-3000A area meter. The leaf samples were then dried at 60°C for five days and weighed to determine LMA (the ratio of leaf dry weight to leaf surface area).

The number of fronds with spores was counted each month from November 1997 through October 1998. Each frond was examined to insure that sori were intact, and no fronds with dehiscent sporangia were counted as fertile.

**STATISTICAL ANALYSIS.**—A one-way ANOVA among all the samples was performed, followed by pre-planned contrasts (Moore and McCabe 1993). Contrasts were used to assess for significant differences in LMA and leaf life span between native and invasive species at low elevation and at high elevation,

and between all natives and the invasive regardless of elevation. Monthly frond production was standardized (number of new fronds produced in a month divided by the maximum number of fronds on the plant). The standardized monthly frond production was used to calculate a standard error of frond production for each species at each site. This standard error was used as a measure of seasonal variation in leaf production (Stratton et al. 2000). The same was done for spore production. Repeated measures ANOVA's were used to analyze yearly data on new frond production, leaf surface area, height growth increase, and spore production. A Tukey's pairwise test was used to determine significance between species.

## RESULTS

The mean height growth of the invasive tree fern *S. cooperi* over the course of one year was significantly greater ( $P < 0.001$ ) than the mean height increase of native tree ferns (Fig. 1). After 11 months of measurements, the mean growth of the invasive tree fern was 15.4 cm, while that of the native tree ferns ranged from 1.9 cm to 3.0 cm. The most valid comparison is between *S. cooperi* and *C. chamissoi* at the same site, where the native tree fern had a mean annual growth of 3.0 cm compared to the 15.4 cm of the invasive tree fern ( $P < 0.001$ ). There were no substantial site-specific differences in height growth among the native tree fern species. An increase in growth during the months of April to August corresponded to an increase in rainfall during this period (Fig. 1).

The number of new fronds produced per month by *S. cooperi* was significantly greater ( $P < 0.001$ ) than the number of new fronds produced by the native tree ferns (Fig. 2). *Sphaeropteris cooperi* produced an average of 2.7 new fronds each month, while the native tree ferns at the same elevation produced an average of 0.4 new fronds per month, and all native tree ferns regardless of elevation produced an average of 0.2 to 0.4 new fronds per month. The native tree ferns also exhibited greater seasonal variation in frond production than *S. cooperi* (Table 2). Seasonality, calculated as the standard error of the standardized monthly frond production, was 2.5 to 3.5 times greater in the native tree ferns compared to *S. cooperi*. A peak in new frond production was observed for the native tree ferns in April, and again in August/September (Fig. 2), however no corresponding peak in leaf surface area per plant was observed as leaf senescence often corresponded with leaf expansion. *Sphaeropteris cooperi* maintained from 12 to 18 fronds per plant over the course of one year. The native tree ferns at all elevations maintained only 3 to 6 fronds per plant over the same time period (data not shown). As a consequence, *S. cooperi* had a higher leaf surface area per plant than the native tree ferns (Fig. 2).

The fronds of low elevation *S. cooperi* had a significantly lower LMA than the native tree ferns growing at the same elevation ( $P < 0.001$ ). Similarly, high elevation *S. cooperi* had a significantly lower LMA than that of native tree ferns growing at high elevation ( $P < 0.001$ ). The fronds of *S. cooperi* had a 1.3 to 3.8 times lower LMA than that of the natives at all sites (Table 2). In addition, the LMA of the native tree ferns tended to increase with increasing ele-

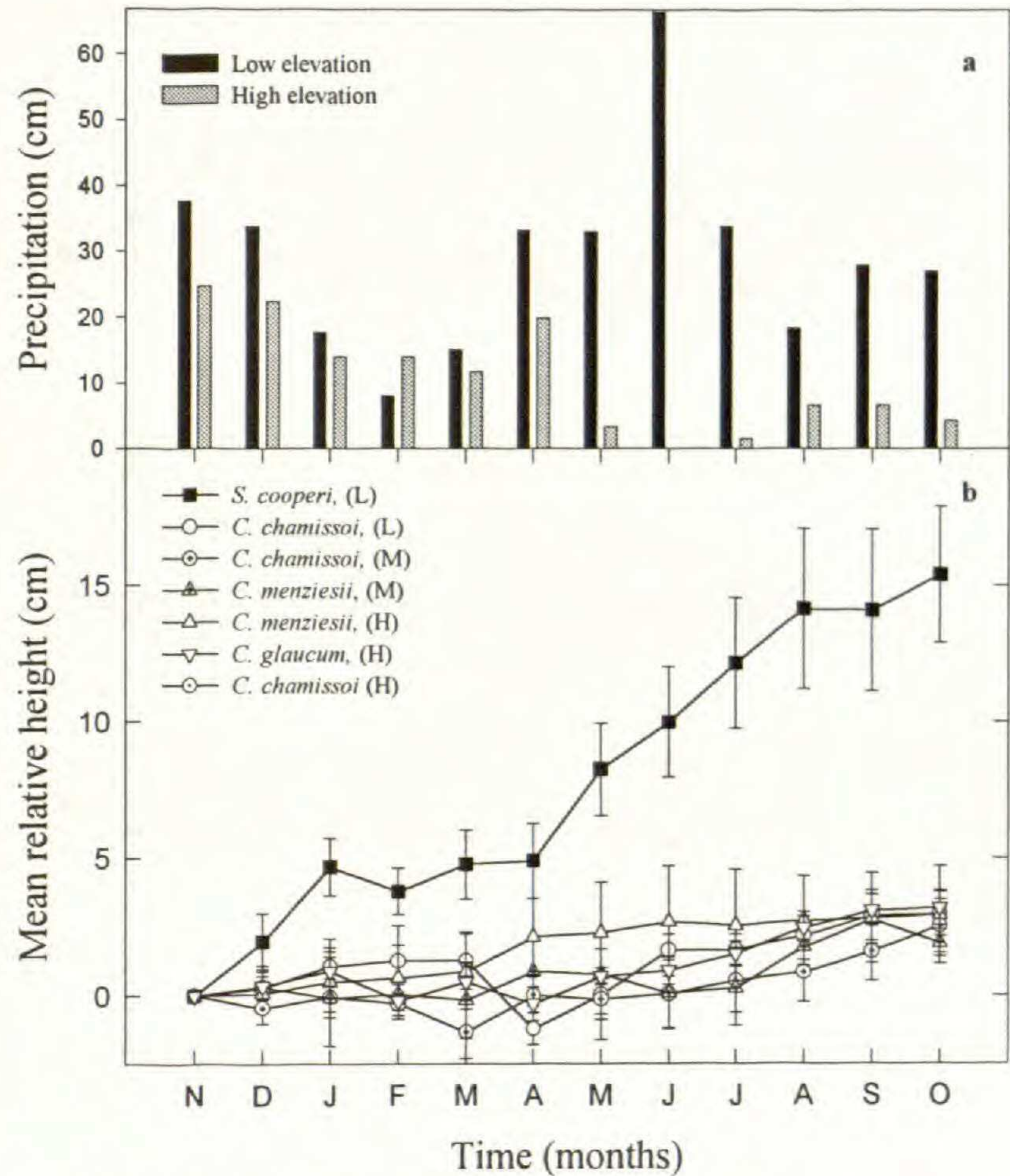


FIG. 1. Seasonal variation in rainfall at the low elevation site (Lyon Arboretum) and high elevation site (Mt. Kaala) on the island of Oahu (a), and mean relative height growth of native and invasive tree ferns (b) over the course of one year, from November 1997 through October 1998. Tree fern height in November was used as a reference. Symbols represent mean  $\pm$  SE (n = 6 to 8). Negative values represent a decrease in height as croziers emerge from the trunk. Filled symbols represent the invasive tree fern *Sphaeropteris cooperi*, and open symbols represent the three native species in the genus *Cibotium*. L, M, and H indicate low, middle, and high elevation study sites. Precipitation data from the National Weather Service.

vation. The leaf life span of low elevation *S. cooperi* was significantly shorter than the leaf life span of the low elevation native tree ferns ( $P < 0.001$ ). The invasive tree fern had 45 to 50 percent shorter leaf life spans than the native tree ferns at all elevations (Table 2).

The number of fertile fronds per plant was significantly greater ( $P < 0.001$ ) in *S. cooperi* than in the native tree ferns (Fig. 3). The invasive tree fern had from 9 to 15 fertile fronds per month, which represented 60 to 75 percent of the total number of fronds per plant. The native tree ferns had between 1 and 4 fertile fronds per month, which represented 20 to 60 percent of the total number of fronds per plant. In addition, the native tree ferns exhibited greater seasonal variation in fertile frond production than *S. cooperi* (Table 2). Seasonality, calculated as the standard error of the standardized mean monthly

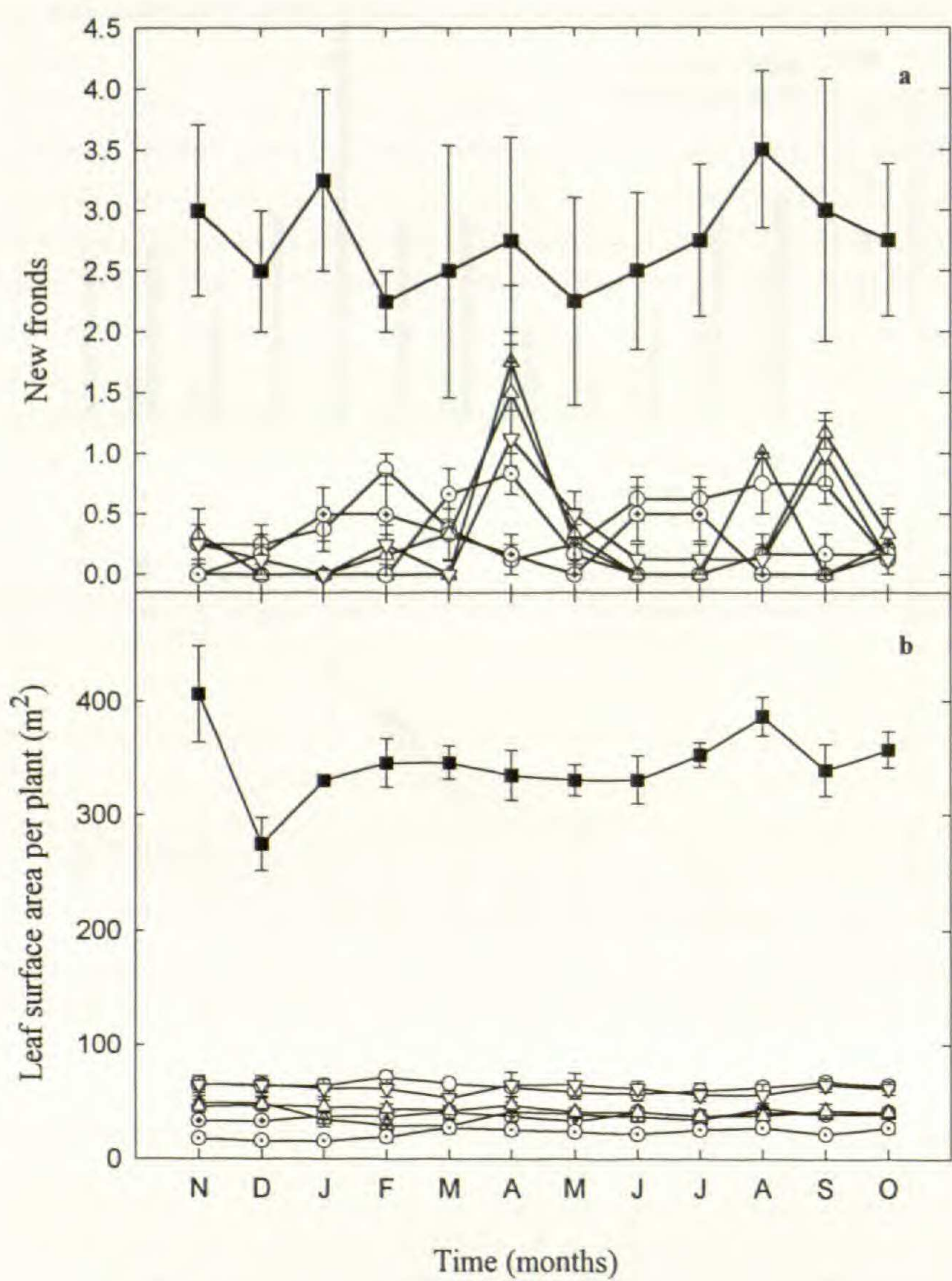


FIG. 2. Number of new fronds produced each month (a) and total surface area per plant (b), from November 1997 through October 1998. Symbols are mean  $\pm$  SE ( $n = 6$  to  $8$ ). Symbols as in Fig. 1. Absence of error bar indicates that the SE is smaller than the symbol.

number of fertile fronds produced per month, was between 20 and 50 percent higher in the native tree ferns (Table 2).

DISCUSSION

Native tree ferns on Oahu (this study) and the island of Hawaii (Walker and Aplet 1994, Wick and Hashimoto 1971) had relatively low annual height increases compared to the invasive tree fern. The Australian tree fern grew very little in January through March, when monthly precipitation was below 20 cm. Growth increased in April through August, apparently as a result of higher precipitation. Growth in the native tree ferns at the low elevation site also increased in April. At the high elevation site we noted that growth showed

TABLE 2. Leaf mass per area (LMA), leaf life span, standard error (SE) of standardized leaf production and of standardized spore production for native and invasive tree ferns at three elevations. Standard error of leaf production is a measure of seasonal variability in leaf production. Standard error of standardized spore production is a measure of seasonal variability in spore production. Values are means  $\pm$  SE. Symbol ( $\dagger$ ) next to a grouping indicates statistical significance ( $P \leq 0.01$ ) between the invasive and native ferns within that group.

		LMA (g m <sup>-2</sup> )	Leaf life span (months)	SE of leaf production	SE of spore production
Low elevation					
Invader	<i>S. cooperi</i>	37.9 $\pm$ 2.1 $\dagger$	6.0 $\pm$ 0.15 $\dagger$	3.35	1.97
Native	<i>C. chamissoi</i>	54.7 $\pm$ 2.8	11.0 $\pm$ 0.30	8.49	3.21
Mid elevation					
Natives	<i>C. chamissoi</i>	50.9 $\pm$ 3.1	12.0 $\pm$ 0.71	11.7	3.66
	<i>C. menziesii</i>	78.9 $\pm$ 4.0	10.8 $\pm$ 1.1	8.32	2.45
High elevation					
Invader	<i>S. cooperi</i>	34.7 $\pm$ 1.8 $\dagger$	n/a	n/a	n/a
Natives	<i>C. chamissoi</i>	120.3 $\pm$ 7.2	10.6 $\pm$ 0.42	9.02	3.46
	<i>C. menziesii</i>	127.5 $\pm$ 3.8	12.0 $\pm$ 0.50	8.72	2.63
	<i>C. glaucum</i>	135.2 $\pm$ 3.0	12.6 $\pm$ 0.73	8.94	4.04

less seasonal variation and may have been influenced by higher irradiance during drier months, when cloud cover is relatively low, as well as by rainfall patterns. Frond production of the native tree ferns also exhibited seasonal variation, with the majority of frond production occurring from February through April. There was virtually no frond production during the months of October, November, and December. This seasonal pattern was similar to the pattern of frond production observed in *Cibotium* on the island of Hawaii by Wick and Hashimoto (1971). In neither study did the pattern of frond production appear to correspond with precipitation. In contrast to the native tree ferns, frond production in the Australian tree fern was consistent throughout the year. The faster growth rate and greater and more consistent frond production of the Australian tree fern *S. cooperi* could contribute to its ability to outcompete the native Hawaiian tree ferns.

When plants of the same growth habit are compared, plants with a higher leaf surface area tend to have a higher relative growth rate (Lambers et al. 1998). *Sphaeropteris cooperi* had over three times more fronds per plant than the native tree ferns, and over four times more leaf surface area (Fig. 2). A greater leaf surface area per plant, along with a greater annual height increase, could allow the Australian tree fern to intercept more light than the native tree ferns, and thus potentially fix more carbon. In a previous study, we observed that the photosynthetic rate at light saturation for shaded plants was between 5 and 7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the invasive tree fern, while the photosynthetic rate at similar light levels was between 3.4 and 4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the native tree ferns (Durand and Goldstein 2001). The pattern of allocation of carbon to different plant organs can also affect the annual height increase of the plant. The native tree ferns have a high starch content in their trunk, and were once harvested for this starch (Ripperton 1924, Wick and Hashimoto

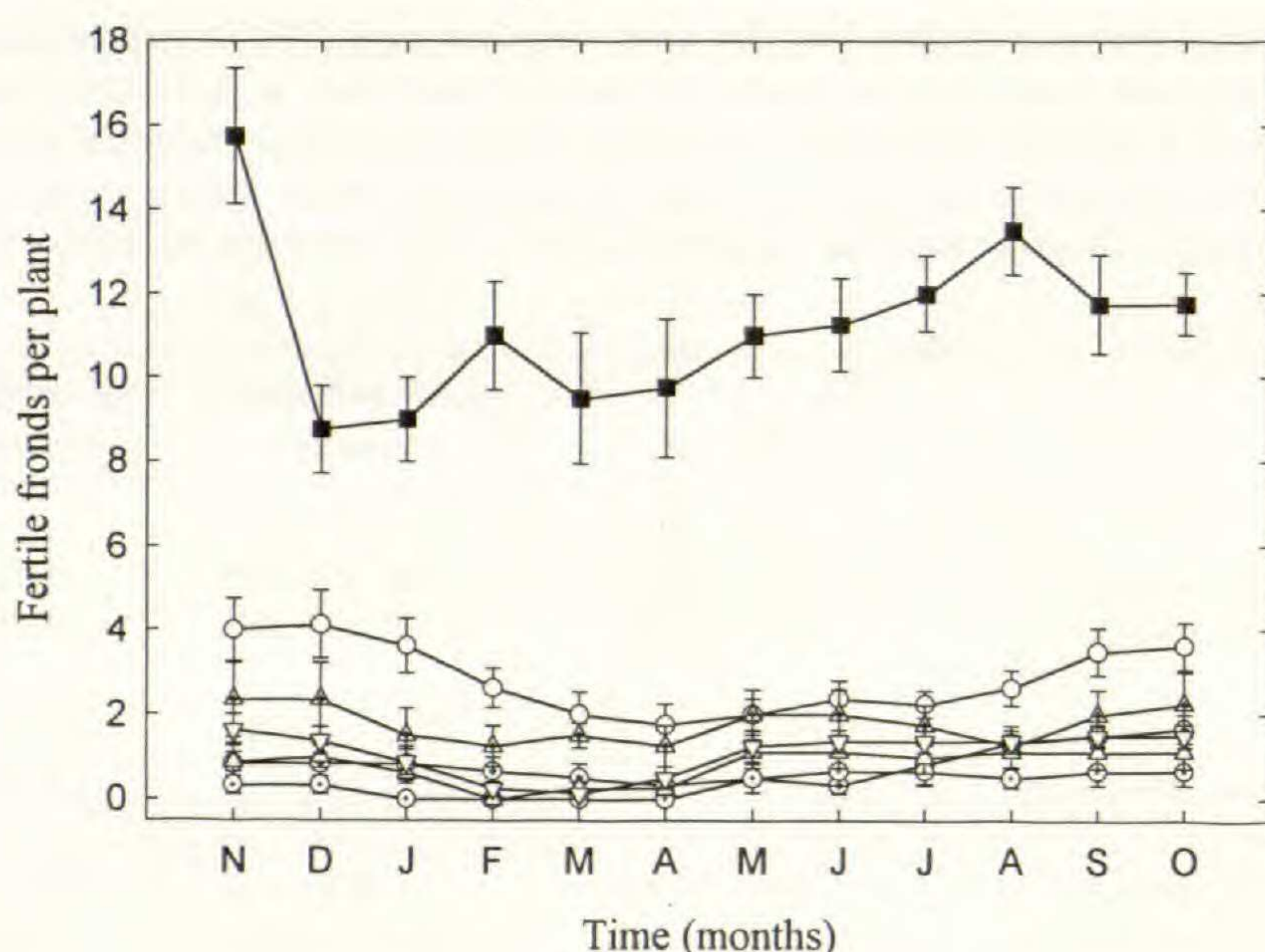


FIG. 3. The number of fertile fronds (with spores) per plant of native and invasive tree ferns, measured from November 1997 through October 1998. Symbols represent  $\pm$  SE ( $n = 6$  to 8). Symbols as in Fig. 1.

1971). While no data is available on the trunk starch content of *S. cooperi*, in areas where *S. cooperi* and *C. chamissoi* grow together, wild pigs preferentially feed on the trunk starch of the native tree ferns. Thus, another possible explanation for the low annual height increase of the native tree ferns is a relatively large allocation of carbon, in the form of starch, to the fern's trunk.

The native tree ferns exhibited seasonal changes in fertility, with the greatest number of fertile fronds present in the months of September through February. The invasive tree fern did not exhibit as much seasonal variation in fertility, though there were more fertile fronds per plant in the months of July through November. The difference in seasonal spore production may allow spores of the Australian tree fern to germinate at a time when spores of the native tree ferns are not available. It has been suggested that successful invasive species either utilize resources more efficiently, or at a time when natives are inactive or unable to access the resources (Vitousek 1986). Consistent monthly spore production could give the Australian tree fern a reproductive advantage over the native tree ferns.

Ferns in the genus *Sphaeropteris* produce 64 spores per sporangium (Gastony 1974), as do ferns in the genus *Cibotium* (Sporne 1966). Dyer (1979) estimated that an average fertile frond of *Cibotium chamissoi* produces 700,000,000 spores. With between 1 and 4 fertile fronds produced per plant per year (Fig. 3), spore production per year ranges between 700 million and 2.8 billion spores. *Sphaeropteris cooperi* produced between 22 and 27 fertile fronds per plant per year (Fig. 3), though the number of sporangia produced per frond is not known. However, this species has a greater frond surface area than *Cibotium*, and given the equal number of spores per sporangia in *Cibotium* and *Sphaeropteris*, assuming equal spore production per frond seems a

conservative estimate. If *S. cooperi* does indeed produce an equal number of spores per frond as *Cibotium chamissoi*, this fern has the potential to produce 15.4 billion to 18.9 billion spores per year. While both species produce a large number of spores each year, *S. cooperi* can potentially produce 13 to 16 billion more spores per year. Studies of the spore production of the invasive tree fern, and spore viability of both the native and invasive tree ferns, need to be conducted in order to have a more complete understanding of the relative reproductive capacity of these ferns.

Variation in leaf life span has been found to be an important predictor of numerous plant responses (Chabot and Hicks 1982, Reich *et al.* 1992, Reich *et al.* 1997). The leaf life span of higher plants can range from less than one month to 25 years (Chabot and Hicks 1982). When compared across diverse ecosystems and biomes, a short leaf life span is associated with factors such as higher photosynthetic rate, higher leaf nitrogen content, lower leaf construction cost, and a lower LMA (Chabot and Hicks 1982, Reich *et al.* 1992, Reich 1993, Reich *et al.* 1997). The mean leaf life span of the Australian tree fern was significantly shorter than the mean leaf life span of the native tree ferns (Table 2). As expected for a plant with a shorter leaf life span, the Australian tree fern had a significantly lower LMA than the native tree ferns (Table 2). Generally, longer-lived leaves require more secondary compounds to protect the leaves against herbivores and pathogens, whereas shorter-lived leaves with a low LMA are able to maximize photosynthetic return per unit weight of the leaves (Lambers *et al.* 1998, Reich 1993). The Australian tree fern produced short-lived leaves with high leaf nitrogen and high photosynthetic capacity (Durand and Goldstein 2001) at a relatively low carbon cost to the plant compared to the native tree ferns. In a recent study of 34 native and 30 invasive higher plants in the Hawaiian Islands, it was found that the latter had lower LMA, higher leaf nitrogen, and higher photosynthetic rates (Baruch and Goldstein 1999). The patterns observed with the ferns in this study were consistent with the pattern found in higher plants, suggesting that this suite of traits are important determinants of the success of invasive species in the Hawaiian Islands, for both ferns and higher plants alike.

The difference in leaf life span, LMA, growth rate, and spore production between the invasive and native tree ferns suggests that there are differences in life history characteristics. Tree ferns in Costa Rica that grew as pioneer species in secondary forest had higher leaf turn-over rates, faster growth rates, and more rapid production of sori than tree ferns that grew in primary forest (Bittner and Breckle 1995). Similarly, the high leaf turn-over rate, high spore production, and rapid growth rate in *S. cooperi* suggests that it tends to behave as a pioneer, or *r* selected species. The native tree ferns, on the other hand, had a much lower leaf turnover rate and slower growth rates, as well as lower reproductive output. This difference in life history characteristics may partially explain why *S. cooperi* can become established and spread quickly in Hawaiian rainforests, particularly in areas of disturbance.

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